Cortical regions responding to eye movement

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1 Introduction

Monitoring the changes in eye position of another should be very important for humans motion perception in general has been well studied in primates. The middle temporal area (MT), or V5, is consistently responsive to all forms of motion, including apparent motion [1]. Apparent motion is the perception of motion generated by changing the spatial position of a stimulus rapidly in time. Recent human neuroimaging studies, using positron emission tomography (PET) [2], functional magnetic resonance imaging (fMRI) [3,4] and magnetoencephalography (MEG) [5-9], indicate a general motion-sensitive region located at the occipito-temporal border thought to be a human MT/V5 homologue. Similarly, real images of apparent facial motion, indicating eye gaze deviations, activate regions of the human superior temporal sulcus (STS), as well as MT/V5 [4], suggesting that the human brain also possess a motion analysis system made up of a number of discrete brain regions. Recently, we reported the MEG responses when viewing eye movement [10], and we summarized the results in that paper in this article.

2 Methods

We studied twelve right-handed volunteers (3 females, 9 males) ranging in age from 26 to 39 years (mean age, 31.5 years) with normal or corrected visual acuity.

We presented stimuli previously used by the Yale group [4] in an experimental paradigm that was slightly modified for MEG studies. The three different stimulus conditions (Fig. 1) were: EYES: In this condition a colored face, superimposed on a radial pattern of three concentric black, white, and gray rings, initially gazed at the viewer. The eyes then suddenly deviated to the right. SIM: In this simulated eye movement condition, colored checks moved in the same part of the visual field as in EYES, and with identical timing. RADIAL: In this condition, the face with eyes gazing at the viewer remained unchanged. However, the pattern of the background rings changed between S1 and S2, producing a percept consisting of an inwardly moving radial stimulus. A fourth stimulus type, which was consisted of a scrambled image of the face on the radial background, was presented as a filler between stimulus conditions. S2 followed S1 with no interstimulus interval. S1 was shown for 800 msec, as was S2. A filler stimulus was presented for a random interval of 1,000 – 1,100 msec between each stimulus condition.

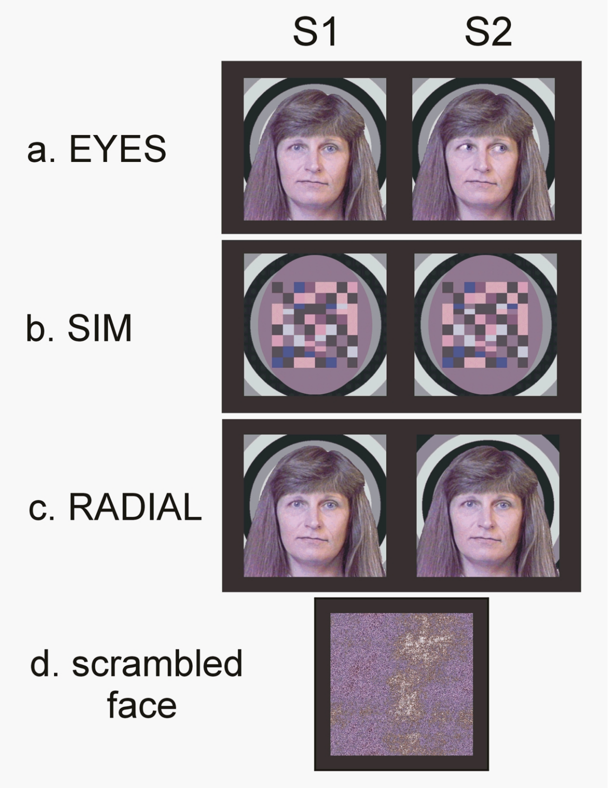

Figure 1: *An example of a stimulus sequence shows the three stimulus conditions interspersed by the interval stimulus relative to recording periods. a. EYES: Eye movement from the center (S1) to the viewer's right (S2). b. SIM: Moving checks simulating eye movements occurred in a similar region of the visual field as EYES. c. RADIAL: Inward radial background movement from S1 to S2. d. The interval stimulus was a scrambled face.*

The distance between the subject's eyes and the display was 160 cm. Stimuli were projected centrally, and subtended a visual angle of 9.7 x 9.7 degrees. Subjects were asked to look at the midway point between the eyes of the face in EYES and RADIAL, and the corresponding spatial point in SIM. The luminance of the center (fixation) point of the face was about 19.2 cd/m^2. All subjects reported experiencing a percept of real motion from the three apparent motion conditions. Since subjects saw a continuously present face between S1 and S2, activity in the fusiform gyrus, known to activate to face onset [11,12] could be minimized. Therefore, cortical responses to movement could be predominantly isolated. A set of 50 trials for each condition was divided into 10 sessions with 4-6 stimuli in each.

MEG was measured with a 37-channel biomagnetometer (Magnes, Biomagnetic Technologies Inc. (BTi), San Diego, CA). The device was 144 mm in diameter and the outer coils were 72.5^0 apart. The probe was positioned at the back of the subject's head overlying the occipito-temporal area in both hemispheres in all subjects. MEG responses were recorded with a bandpass of 0.1-50 Hz and digitized at a sampling rate of 1,024 Hz. We used an extended analysis window of 300 msec before and 1,500 msec after S1 onset, but mainly concentrated on the components following S2 onset, that is, from 800 msec after S1 onset.

A spherical model was fitted to the digitized shape of the head of each subject and the best-fitted equivalent current dipole (ECD) was estimated. We used not only single, but also double ECD software generated by BTi [13]. Both single and double ECD models were based on the report of Sarvas [14] using the nonlinear inverse problem and dipole location. We used an analysis of variance (ANOVA) with the post-hoc test (Fisher's protected least significant difference (PLSD)), and P<0.05 for identifying significant results.

3 Results

As right-sided MEG activity was the clearest and most predominant, we focused our analysis on the right hemisphere in this article. S2 onset produced a large clear component termed the first magnetic response, or 1M (Fig. 2). The reliable ECDs of 1M to S2 were estimated to both EYES and RADIAL stimulus in only 6 out of 12 subjects. Although large 1Ms were identified to SIM in same 6 subjects, the SIM 1M waveforms were complex relative to those of EYES and RADIAL, and their peaks were not clearly identifiable in some subjects. Therefore, we statistically analyzed results in the 6 subjects who showed a clear 1M to EYES and RADIAL.

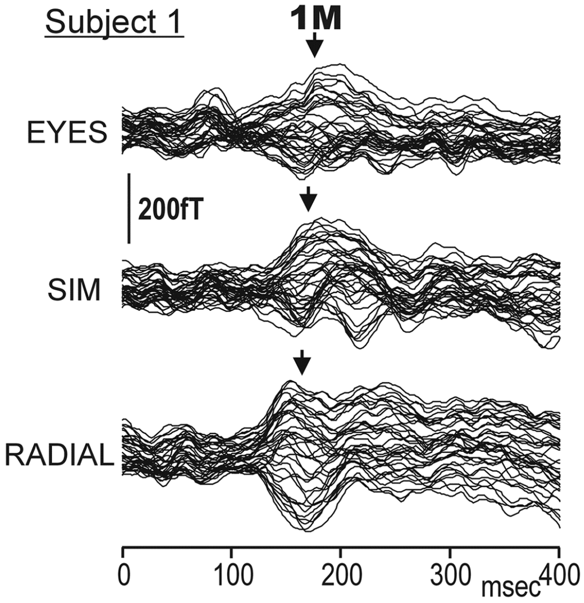

Figure 2: *MEG waveforms in subject 1 in response to the three conditions. A large clear component, 1M, was identified for all conditions in this subject in the superimposed MEG waveforms recorded from 37 channels in the right hemisphere. 1M was larger and earlier for RADIAL relative to EYES and SIM. The waveform of the 1M to SIM was relatively complex relative to that of EYES and RADIAL.*

Peak 1M latency was 192.4 ± 42.4 msec and 161.7 ± 36.5 msec for EYES and RADIAL, respectively, following S2 stimulation. The effects of the stimulus type were significant (P<0.01). Post-hoc paired comparisons using Fisher's PLSD showed that the latency of the 1M to RADIAL was significantly shorter than the 1M to EYES (P<0.05). The dipole moment (Q) of the 1M to EYES, 13.5 ± 7.0 nAm, was smaller than that to RADIAL, 27.0 ± 17.0 nAm. The dipole moments were also submitted to repeated-measures ANOVA with factors of a stimulus type (EYES and RADIAL), but the effect of the stimulus type was not significant. The ECD of the major source in response to EYES was located very close to that for RADIAL in each subject, although there was a tendency for the former to be positioned slightly posterior and inferior to that of the latter. They were located around the occipito-temporal border, which is considered to be the MT/V5 homologue in humans, in all subjects (Fig. 3). The 1M to SIM showed a reliable ECD in only subject 1 and was located close to those for EYES and RADIAL (Fig. 3).

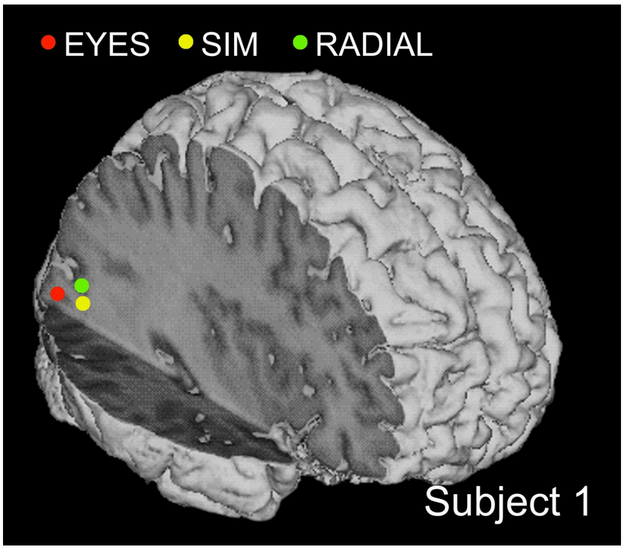

Figure 3: *The ECDs of the 1M to EYES, SIM and RADIAL recorded from the right hemispheres in subject 1. The ECDs were located around the occipito-temporal border, along the ITS, in human MT/V5. The ECD location was more posterior and inferior for EYES than RADIAL and that for SIM was located in the neutral area between EYES and RADIAL.*

ECD x, y and z coordinates were submitted to repeated-measures ANOVA with a factor of stimulus type (EYES and RADIAL). The effects of stimulus type were significant ($P<0.01$). Post-hoc paired comparisons using Fisher's PLSD showed that the x- and z-value of the 1M to EYES was significantly posterior and inferior than the 1M to RADIAL ($P<0.05$), although its mean difference was only 7 mm.

4 Discussion

Robust 1M MEG components were obtained from the region MT/V5, and this region did not generate significant responses at other latencies. If the STS is indeed a higher order motion area, then it is conceivable that the STS activation using fMRI reported by Puce et al. [4] reflects activity occurring several hundred milliseconds later. Preliminary data with intracranial ERP recordings to facial motion stimuli using mouth movements indicate that regions of the STS produce predominant ERP components at around 400ms post-stimulus [15]. On the other hand, if posterior regions of the STS do generate activity in the 1M latency range, ECD location as estimated by MEG should be at the center of the activated areas. If both STS and MT/V5 areas are activated simultaneously but the activity in the MT/V5 at around 150-200 msec post-movement onset are much larger than that in the STS, the net ECD would occur in or near MT/V5. Taken together, the results of the fMRI and MEG study, suggest that the earliest prominent regions of activation responsive to viewing eye gaze deviations at around 150-200 msec occur in MT/V5 are probably independent of the region in MT/V5 activated by radial background movement.

Our ECD centers for EYES and RADIAL had a separation distance of around 1 cm. Given that additional contributions to the 1M response from STS and V1 were ruled out as being unlikely, an interesting question arises regarding the two separate sources of activation to EYES and RADIAL in MT/V5. Given that the RADIAL stimulus was extrafoveal compared to our parafoveal EYES stimulus, the question arises whether the difference in centers of activation is a function of retinotopy in human MT/V5? Tootel et al. [3], using fMRI, concluded that human MT/V5 has a similar magnification factor to V1 for peripheral versus central stimulation.

However, they were unable to demonstrate a systematic difference in activation pattern for peripheral versus central stimulation. In our study, ECD to parafoveally presented eye movements was located more posterior and inferior to that to the extrafoveal radial movement shown in the peripheral field. It is possible that MEG may be a more sensitive technique by which to investigate these issues.

With regard to the waveform analysis, the most interesting finding was that the 1M to RADIAL was shorter in latency and larger in amplitude than that to EYES. This finding further underscores the putative differences between the peripherally presented and centrally presented RADIAL and EYES stimuli. If the RADIAL stimulus preferentially activated the magnocellular system, then conceivably the information could take alternative routes via the superior colliculus and pulvinar to the extrastriate cortex directly, as well as through V1 [16], unlike EYES which would take the route through striate cortex. Given that the magnocellular system has faster response properties, it is conceivable that neuronal responses mediated by this pathway could occur earlier than those mediated by the parvocellular pathway. Hence, we would expect to observe an earlier response to our RADIAL stimulus when compared to that for EYES.

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